

# Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002

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## Abstract

We tested the hypothesis that increased growth of salmon during early marine life contributed to greater survival and abundance of salmon following the 1976/1977 climate regime shift and that this, in turn, led to density-dependent reductions in growth during late marine stages. Annual measurements of Bristol Bay (Bering Sea) and Chignik (Gulf of Alaska) sockeye salmon scale growth from 1955 to 2002 were used as indices of body growth. During the first and second years at sea, growth of both stocks tended to be higher after the 1976–1977 climate shift, whereas growth during the third year and homeward migration was often below average. Multiple regression models indicated that return per spawner of Bristol Bay sockeye salmon and adult abundance of western and central Alaska sockeye salmon were positively correlated with growth during the first 2 years at sea and negatively correlated with growth during later life stages. After accounting for competition between Bristol Bay sockeye and Asian pink salmon, age-specific adult length of Bristol Bay salmon increased after the 1976–1977 regime shift, then decreased after the 1989 climate shift. Late marine growth and age-specific adult length of Bristol Bay salmon was exceptionally low after 1989, possibly reducing their reproductive potential. These findings support the hypothesis that greater marine growth during the first 2 years at sea contributed to greater salmon survival and abundance, which in turn led to density-dependent growth during later life stages when size-related mortality was likely lower. Our findings provide new evidence supporting the importance of bottom-up control in marine ecosystems and highlight the complex dynamics of species interactions that continually change as salmon grow and mature in the ocean. © 2007 Elsevier Ltd. All rights reserved.

**Keywords:** Salmon; Growth; Survival; Competition; Climate change; North Pacific Ocean

## 1. Introduction

Many species in the Bering Sea and North Pacific Ocean underwent significant changes in abundance

following the 1976–1977 climate shift (Beamish and Bouillon, 1993; Mantua et al., 1997). This shift was associated with a pronounced increase in the size and intensity of winter storms, which, in turn, resulted in an increase in winter sea-surface temperature (SST) in some northern regions. Following the transition, the abundance of some species assemblages increased (zooplankton, Pacific salmon, and groundfish) whereas others decreased

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(crustaceans, forages fishes, piscivorous birds, and pinnipeds) (Rogers, 1984; Alverson, 1992; Francis et al., 1998; Anderson and Piatt, 1999). During winter 1988–1989, another regime shift occurred in some components of the eastern North Pacific ecosystem (Hare and Mantua, 2000). In 1997, unusually warm SSTs and calm winds during summer had a profound impact on Bering Sea biota (Kruse, 1998; Napp and Hunt, 2001). Some evidence suggests that another regime shift occurred in 1998, but its effects on biota were greatest in southern regions (King, 2005). During 2001–2003, summer temperatures in the southeastern Bering Sea were exceptionally warm and, if they continue, could result in a shift from Arctic to sub-Arctic species (Overland and Stabeno, 2004). While climate shifts affect large geographical areas, regional differences in species responses to the shifts can be significant (King, 2005; Pyper et al., 2005).

Various hypotheses have been developed to explain the complex responses of species to shifts in oceanographic conditions in the North Pacific Ocean and Bering Sea (Gargett, 1997; Francis et al., 1998; Anderson and Piatt, 1999; Hollowed et al., 2001; Ware and Thomson, 2005). Building upon these hypotheses, Hunt et al. (2002) proposed the oscillating control hypothesis (OCH), which predicted that the pelagic ecosystem in the southeastern Bering Sea alternates between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. The OCH predicts that salmon abundance in the southeastern Bering Sea may increase during warm regimes in response to greater prey abundance.

Total abundance of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean increased sharply from approximately 300 to 700 million adult salmon per year following the 1976–1977 climate shift, largely as a result of increases in northern regions (Rogers, 1987, 2001). Mechanisms leading to this increase in salmon abundance are largely unknown, but researchers have assumed that greater prey biomass in the ocean was a key factor (Francis et al., 1998; Beamish et al., 1999). Brodeur and Ware (1992) reported significantly greater biomass of zooplankton in the Gulf of Alaska after the mid-1970s, but no zooplankton biomass increase was detected in the southeastern Bering Sea where numbers of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) significantly increased (Napp et al., 2002). However, based on cohort analysis, age-0 pollock (*Theragra chalcogramma*) were exception-

ally abundant (Hunt et al., 2002), and young pollock may have contributed to the diet of sockeye salmon (Farley et al., 2005). Increases in salmon prey abundance in response to climate change are not well documented because Pacific salmon opportunistically consume a variety of prey that changes with their size, and because annual growth at sea of immature salmon is rarely measured. Prey species include squid, small fishes and euphausiids that are difficult to quantify, both in terms of abundance in the ocean and in the diet of salmon, which are distributed across broad oceanic regions (Percy et al., 1988; Cooney and Brodeur, 1998; Kaeriyama et al., 2004).

Although it is plausible that greater prey biomass caused greater salmon abundance after the 1976/1977 climate shift, the influence of prey biomass is complicated because size at age of adult salmon declined throughout most of the Pacific Rim during the past 30 years, suggesting that food availability limited rather than enhanced salmon growth (Peterman, 1984; Bigler et al., 1996; Cox and Hinch, 1997; Kaeriyama, 1998; Pyper and Peterman, 1999). Adult salmon abundance and mean size were inversely correlated with indices of zooplankton abundance in the Gulf of Alaska (Cooney and Brodeur, 1998), suggesting that salmon may reduce zooplankton abundance. Welch et al. (1995) hypothesized that warming SSTs in the North Pacific Ocean may cause salmon distribution to shift northward, resulting in a smaller foraging area and greater density dependence. Declining salmon size at age has raised concern regarding the capacity of the ocean to support wild salmon populations while hatcheries release approximately 5 billion juvenile salmon per year into the North Pacific Ocean (Cooney and Brodeur, 1998; Mahnken et al., 1998).

Alternative hypotheses on mechanisms leading to greater salmon abundance have been proposed. These include a shift in the diets of predators away from salmon in response to increasing abundance of alternative prey (Percy, 1997), or a change in the distribution of salmon relative to their predators (Rogers, 1984). Uncertainty regarding the mechanism(s) leading to greater salmon abundance also stems from the absence of data on numbers of salmon smolts leaving freshwater habitats prior to the mid-1970s (Bradford, 1995). Furthermore, the potential for increased salmon production from freshwater habitats in response to climate change is largely unknown (Hilborn et al., 2003).

We hypothesize that the large increase in Alaskan sockeye salmon abundance after the 1976–1977 climate shift was related to faster growth during early marine life stages. This led to density-dependent growth during later life stages when growth-related mortality was likely low (Ricker, 1976). We tested the hypothesis by comparing abundances of adult sockeye salmon with adult length at age of Bristol Bay sockeye salmon and indices of annual growth at sea of Bristol Bay (Bering Sea) and Chignik (Gulf of Alaska) sockeye salmon from the 1950s to early 2000s. We also examined sockeye salmon growth in response to the 1976–1977 and 1989 climate shifts and to climate conditions in 1997 and 2001–2003.

## 2. Methods

### 2.1. Salmon growth measurements

Body growth was determined by measuring the widths of annual growth rings on fish scales collected from adult sockeye salmon originating from Bristol Bay (southeast Bering Sea) and Chignik (south side of Alaska Peninsula). The smolts of both regions migrate to the ocean primarily during May and June after spending typically 1 or 2 years in freshwater (Rogers, 1988; Ruggerone, 2003). Bristol Bay salmon inhabit the southeastern Bering Sea during their first growing season, whereas Chignik sockeye salmon enter the Gulf of Alaska. The distribution of Bristol Bay sockeye salmon overlaps that of Chignik sockeye salmon during the second and third years at sea, although Bristol Bay salmon tend to be distributed farther west, and some Bristol Bay sockeye salmon occupy the central Bering Sea during summer (French et al., 1976; Myers et al., 1996).

Previous studies have shown that the growth of salmon scales provides an index of annual and seasonal growth of salmon at sea (Fukuwaka and Kaeriyama, 1997; Fisher and Percy, 2005). Adult salmon scales were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska, and from the School of Aquatic and Fishery Sciences, University of Washington. We selected scales from sockeye salmon sampled in the Kvichak and Egegik rivers and from Chignik Lagoon to reduce the possibility of mixed stocks in the scale collection (Ruggerone et al., 2005). Equal numbers of male and female salmon were examined each year to prevent bias associated with differential

growth of male and female salmon (Lander and Tanonaka, 1964).

Average scale growth during each year at sea was measured independently from four age groups of Kvichak River sockeye salmon (ages 1.2, 1.3, 2.2, and 2.3), three age groups of Egegik River sockeye salmon (ages 1.3, 2.2, and 2.3), and the two dominant age groups of Chignik sockeye salmon (ages 1.3 and 2.3). These age designations identify the number of winters in freshwater after emergence (e.g., 1.x), followed by winters in the ocean (e.g., x.3). Scales from Bristol Bay sockeye salmon were collected and measured annually from the 1950s to 2002, and scales from Chignik sockeye salmon were collected from the 1950s to 1997. Each year, approximately 50 scales were measured from each age group and stock of Bristol Bay salmon and 100 scales per age group of Chignik salmon. The total number of scales measured in 1 year was up to 550. Scales were admitted to this study based on the following criteria: (1) agreement with the age determination previously made by ADFG, (2) the scale shape indicated the scale was taken from the “preferred area” (Koo, 1962), and (3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis.

Procedures for measuring scale growth followed Davis et al. (1990) and Hagen et al. (2001). After selecting a scale, the entire scale was scanned from a microfiche reader and stored as a high-resolution ( $3352 \times 4425$  pixels) digital file. This resolution was sufficient to distinguish narrowly spaced circuli; a requirement for making accurate measurements of scale growth. The digital image was loaded in Optimas<sup>®</sup> 6.5 image processing software to measure distances between circuli using a customized but standardized program. Each scale image was displayed on a digital LCD flat panel tablet. The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first salt water annulus (Fig. 1). The distance (mm) between each circulus was measured. Annual growth of the first freshwater annulus (FW1) was measured as the distance from the focus of the scale to the outer edge of the last circulus of the first year of freshwater growth. Growth that occurred during a second year in freshwater (FW2) was the distance between the end of the first freshwater zone and the outer edge of the last circulus of the second freshwater annulus. Spring plus-growth (FWPL) was measured to account for

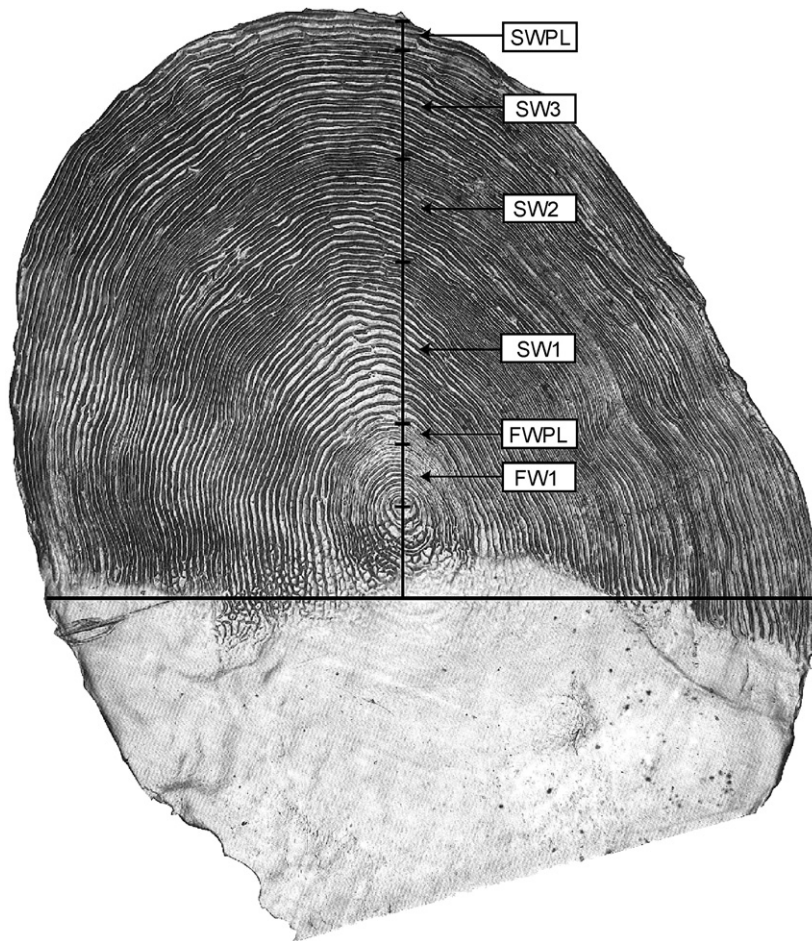


Fig. 1. Age-1.3 sockeye salmon scale from Bristol Bay showing the measurement axis and life stage zones corresponding with growth during the first (SW1), second (SW2), and third (SW3) years at sea, and during the homeward migration (SWPL).

scale growth that occurred in freshwater after the winter annulus had been laid down until marine growth began in the sea in spring. Likewise, each annual ocean growth zone (SW1, SW2, and SW3) was measured as the distance between the last circulus forming each growth zone. The final ocean growth zone (SWPL) was measured from the circulus that forms the outer edge of the last annulus on the scale to the scale margin. As these fish spawn and die in the fall, no annulus records the final spring/summer of growth. Mean body length of adult Bristol Bay sockeye salmon, 1958–2003, was calculated from mean lengths of the nine stocks that produce the large majority of Bristol Bay sockeye salmon. Mean length of each stock was calculated from the mean of each age group (ages 1.2, 1.3, 2.2, and 2.3) and sex (Rogers and Ruggerone, 1993; Ruggerone et al., 2003).

Average scale growth during each phase of marine life (SW1, SW2, SW3, and SWPL) was used to assess age-specific year-to-year growth trends, to compare with abundances of sockeye salmon returning to western and central Alaska, and to compare growth with an index of Bristol Bay sockeye salmon productivity (described below). Representative indices of the growth of Bristol Bay sockeye salmon were calculated by taking the average values of measurements from two Bristol Bay stocks (Kvichak and Egegik). When calculating the average growth of the two stocks at each life stage (e.g. SW1), the age groups (ages 1.2, 1.3, 2.2, and 2.3) contributing to that average were equally weighted. Had the growth histories of the stocks been independent, taking their average as an index of regional growth would have made little sense. However, if their growth at sea was positively



correlated, it is an indication that the stocks shared at least some aspects of their ocean environment in common. We found that stage-specific scale growth measurements from each age group were significantly correlated among stocks ( $P < 0.05$ ), except for only one of the 10 comparisons involving the three stocks ( $P = 0.07$ ).

A second group of annual growth indices was calculated from the mean of Bristol Bay and Chignik salmon scale measurements. These indices were intended to represent the average growth of sockeye salmon in the Bering Sea and North Pacific Ocean. Sockeye salmon originating from Bristol Bay and Chignik are known from tagging studies to be widely distributed in the Bering Sea and North Pacific Ocean, and there is considerable overlap among all stocks originating from western and central Alaska (French et al., 1976; Myers et al., 1996). We found that mean scale growth of Kvichak, Egegik, and Chignik sockeye salmon were positively correlated during each year at sea, except for growth of Chignik and Kvichak salmon during the homeward migration (SWPL) (Table 1). Thus, combining scale growth measurements from age groups and stocks provided relatively robust indices of sockeye marine growth in the Bering Sea and North Pacific Ocean during each life stage at sea. As the Chignik scale time series ended in 1997, estimates of their growth from 1998 to 2002 were developed using linear regressions of Chignik growth on Bristol Bay growth.

A third growth index was calculated to compare with the annual estimates of Bristol Bay sockeye salmon productivity, which are computed by brood

year. Nearly, all returning adults migrated to sea after either 1 or 2 years in freshwater, so any particular cohort produced smolts that entered the ocean in adjacent years. Therefore, ocean growth indices for the two life-history types of the same cohort are offset by 1 year. To accommodate the variable proportions of the two life histories in a single cohort, mean scale growth for a cohort was weighted by the proportion of adults of a cohort returning from age 1 or age 2 smolts. Thus, the mean growth of the dominant smolt age group had more influence on the growth measure of interest.

## 2.2. Salmon abundance and productivity data

Annual estimates of adult sockeye salmon abundance (run size) in western and central Alaska were obtained from annual reports of the ADFG (L. Fair, pers. comm.). Most sockeye salmon in western Alaska are from Bristol Bay, whereas those in central Alaska include the Chignik, Kodiak, and Cook Inlet stocks. Harvests of eastern Kamchatka pink salmon were obtained from Sinyakov (1998) and the North Pacific Anadromous Fish Commission (K. Myers, pers. comm.). An index of Asian pink salmon abundance (“0” in even years; “1” in odd years) was compared with sockeye salmon abundance and productivity because pink salmon have a 2-year life cycle and they are much more abundant in the region inhabited by western Alaska sockeye salmon during odd-numbered years (Sugimoto and Tadokoro, 1997; Ruggerone and Nielsen, 2004).

Table 1

Correlation coefficients ( $r$ ) of Kvichak (Kvi), Egegik (Eg), and Chignik (Chig) scale growth (upper triangle) during each life stage at sea (SW1, SW2, SW3, and SWPL) from the 1950s to the 1990s

Stage	SW1			SW2			SW3		
Stock	Kvi	Eg	Chig	Kvi	Eg	Chig	Kvi	Eg	Chig
Kvichak	1	0.78	0.41	1	0.85	0.61	1	0.85	0.52
Egegik	<0.001	1	0.35	<0.001	1	0.59	<0.001	1	0.77
Chignik	0.007	0.033	1	<0.001	<0.001	1	<0.001	<0.001	1
	SWPL			SW1 + SW2			SW3 + SWPL		
Kvichak	1	0.54	0.17	1	0.84	0.63	1	0.80	0.50
Egegik	<0.001	1	0.61	<0.001	1	0.56	<0.001	1	0.78
Chignik	0.278	<0.001	1	<0.001	<0.001	1	<0.001	<0.001	1

$P$ -values associated with each correlation are shown in the lower triangle. Correlated values are mean of all available age groups for each stock.

An index of Bristol Bay sockeye salmon productivity was calculated for comparison with annual Bristol Bay salmon growth indices. Bristol Bay sockeye salmon stocks spawn in watersheds located on both the east and west coasts of Bristol Bay. Composite Ricker recruitment curves,  $\log_e(R_j/S_j) = a - b(S_j)$ , were estimated using linear regression for each coast, where  $R$  is the sum of all adult returns of the  $j$ th cohort to a coast, and  $S$  is aggregate parental spawner abundance of the  $j$ th cohort on that coast. Only the 1973–1990 brood years were used as this was a period of relatively high and somewhat stable productivity (Peterman et al., 2003). The value of the Bristol Bay productivity index for any brood year was calculated as the average of the two residuals (deviations from the Eastside and Westside Ricker curves) for that cohort, 1952–1997. The index reflects survival after removing density-dependent factors associated with parental and/or juvenile abundances in freshwater (Peterman et al., 1998). Nearly, all Bristol Bay stocks were used in an effort to minimize effects of stock-specific variability and measurement error.

Monthly SST data for the primary region of the North Pacific Ocean occupied by Bristol Bay (55–57°N; 165–157°W) and Chignik (53–55°N; 165–157°W) sockeye salmon during early marine life were derived from COADS data provided by the US National Center for Atmospheric Research and the US National Oceanic and Atmospheric Administration (Woodruff et al., 1998). SST in these two adjacent regions was correlated ( $r = 0.49$ ). Seasonal mean SSTs were calculated for the entire area. For comparison with adult salmon abundance returning to western and central Alaska, SST was lagged 2 and 3 years to correspond with years of smolt migration. Likewise, SST from the southeastern Bering Sea during years of smolt migration was compared with the productivity index of Bristol Bay sockeye salmon.

### 2.3. Data analyses

Statistical models were developed using multiple regressions to evaluate factors associated with adult salmon body length, abundance, and productivity. Discrete variables (0, 1) were used to test the importance of ocean regime shifts in 1976–1977 and 1989 on salmon characteristics. Autocorrelation of model residuals was examined to determine whether the assumption of independent errors was met. Collinearity between independent variables, which

can influence parameter estimates if strong, was examined using tolerance, variance inflation factors (VIF), and eigenvalues. Partial residuals were used to show relationships between dependent and each independent variable while accounting for all other variables in the model (Larsen and McCleary, 1972). Partial residuals display curvilinear relationships, if present. Mean partial residual values were set equal to the mean of the dependent variable.

## 3. Results

### 3.1. Inter-annual scale growth

Growth of Bristol Bay sockeye salmon scales during the first year in the southeastern Bering Sea (SW1) tended to be below average from the early 1950s to 1972, relatively high during 1978 to 1988, and average during 1989 through 2000 (Fig. 2). Sockeye growth immediately following the 1976–1977 climate shift tended to be greater than that during the previous 26 years, suggesting that early marine growth of sockeye salmon in the southeastern Bering Sea responded rapidly to conditions associated with the 1976/1977 climate shift.

Bristol Bay sockeye salmon growth during the second year at sea (SW2) was similar to that during the first year; low during the 1950s and early 1960s followed by an extended period of relatively high growth (Fig. 2). However, growth during the second year began to increase in the mid-1960s and tended to remain above average thereafter. Growth during the second year at sea exhibited a strong alternating-year pattern of growth that was below average in odd-numbered years.

In contrast to the first 2 years at sea, growth of Bristol Bay sockeye salmon during the third year at sea (SW3) tended to be average to above average prior to the mid-1970s, then growth declined and tended to remain below average during 1981–2001 (Fig. 2). A strong alternating-year pattern of growth was also present during the third year at sea except from 1973 to 1983. Growth during homeward migration (SWPL) before re-entry into rivers in July tended to be average to below average from 1955 to 1972, above average during 1973–1982, then below average from 1983 to 1999.

Growth trends of Chignik sockeye salmon (Fig. 3) were correlated with those of Bristol Bay sockeye salmon (Table 1). During the first year in the Gulf of Alaska, Chignik sockeye salmon growth was below

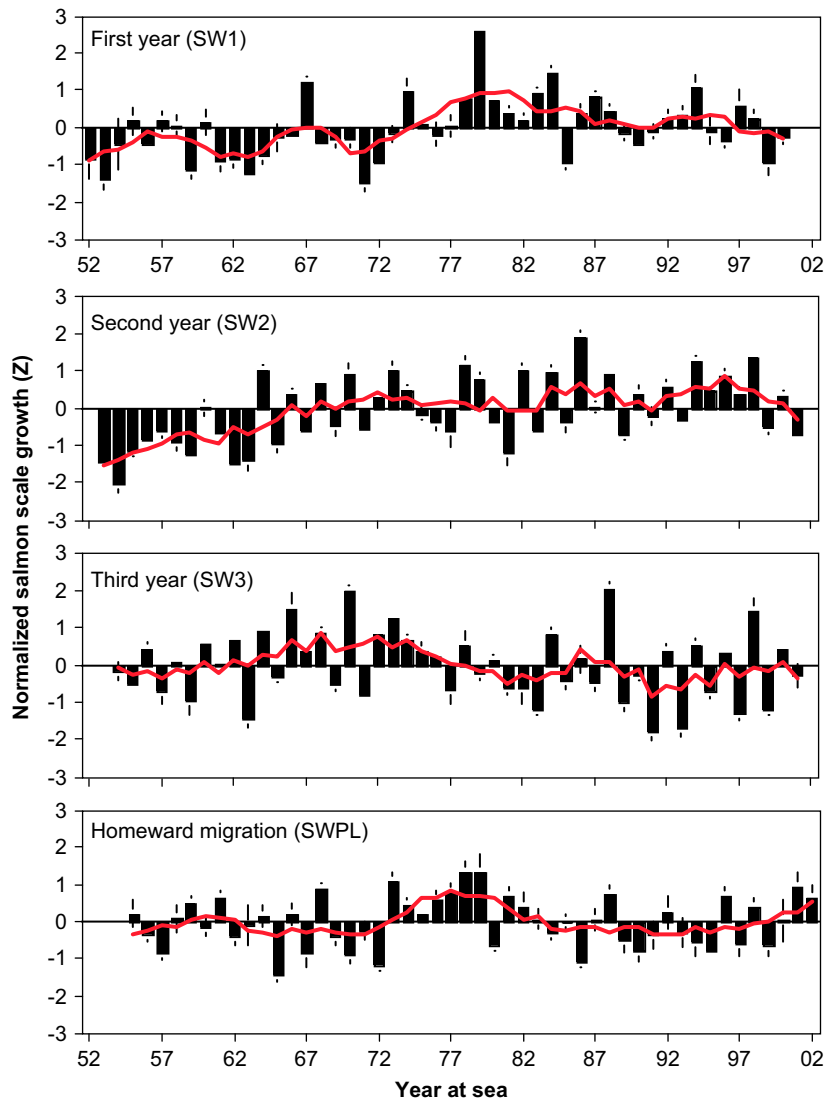


Fig. 2. Growth of Bristol Bay sockeye salmon scales during each year at sea, 1952–2002. Values are mean  $\pm$  1 SE. Line represents the running average of 5 years.

average prior to the late 1960s and consistently above average immediately after the 1976–1977 climate shift. Second-year growth tended to follow a trend that was similar to what was observed during the first year but was below average prior to 1973 and above average after 1977. The difference in growth before and after the 1976–1977 climate shift was much greater during the second year at sea compared with the first year, and this shift in growth was greater than that shown by Bristol Bay sockeye salmon. During the third year at sea, growth was below average during odd-numbered years after 1978, a period when scale growth during the homeward migration also tended to be below average.

Growth of Bristol Bay scales during SW1 and Chignik scales during SW1 and SW2 tended to increase soon after the 1976–1977 climate shift, whereas growth during other life stages began to change before (Bristol Bay SW2, SW3; Chignik SW3) or after the 1976/77 climate shift (e.g., SWPL). Changes in early marine scale growth in response to the 1989 climate shift were less apparent, whereas growth of Bristol Bay salmon during the third year and homeward migration tended to be especially low after 1989 (Fig. 2). Bristol Bay sockeye salmon scale growth did not exhibit extreme growth patterns in response to the unusually warm years of 1997 and 2001–2002.

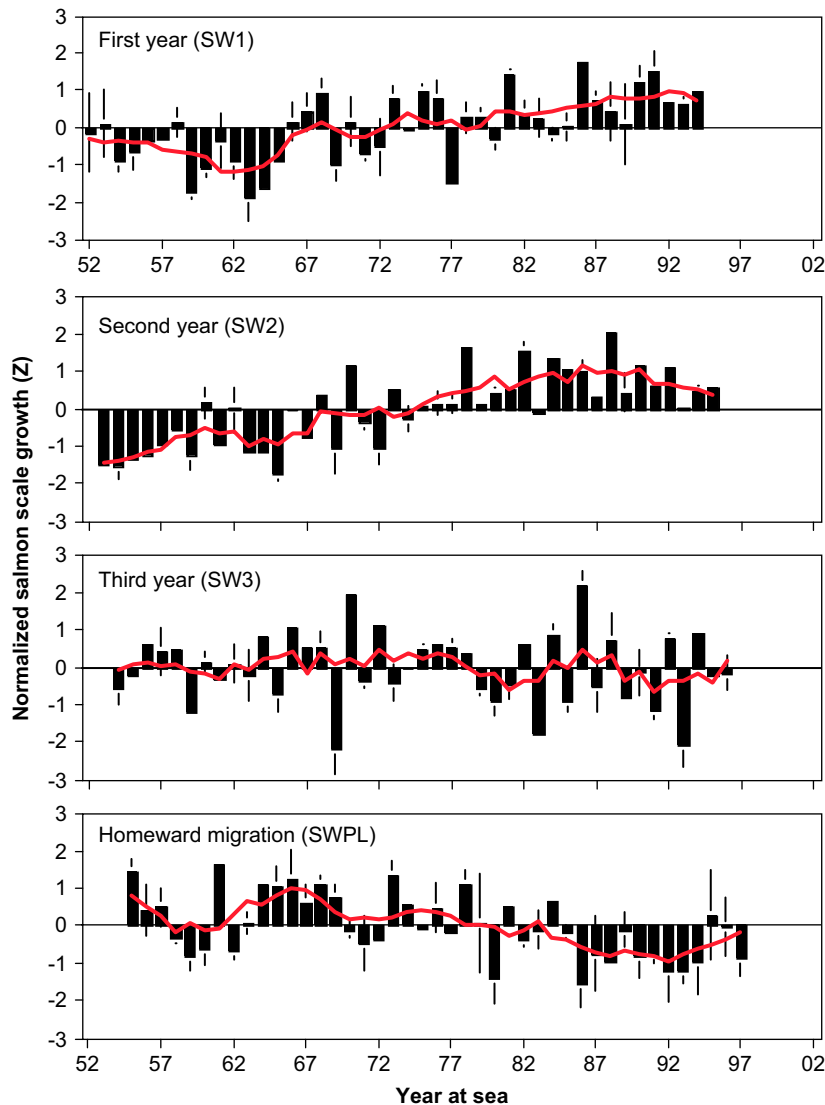


Fig. 3. Growth of Chignik sockeye salmon scales during each year at sea, 1952–1997. Values are mean  $\pm$  1 SE. Line represents the running average of 5 years.

### 3.2. Salmon growth, abundance, and density dependence

Sockeye salmon run size (abundance) in western and central Alaska ranged from 7 to 84 million salmon from 1955 to 2001 (Rogers, 2001). This variation in run size was correlated with variation in salmon growth indices (Fig. 4). The multivariate analysis indicated that run size was positively correlated with both the average of Bristol Bay and Chignik scale growth during the first 2 years at sea and with January to April SST prior to entry into the ocean. Abundance was negatively correlated with

scale growth during the third year, with scale growth during homeward migration, and with an index of pink salmon abundance (Fig. 4). The parameters of the regression model are

$$\begin{aligned} \text{Sockeye abundance (millions)}_i &= 2.46 + 17.88(\text{SW1} + \text{SW2})_i \\ &\quad - 11.78(\text{SW3} + \text{SWPL})_i \\ &\quad - 12.19(\text{pink salmon index})_{i-1} \\ &\quad + 12.18((\text{SST}_{i-2} + \text{SST}_{i-3})/2), \end{aligned} \quad (1)$$

where  $i$  is the year of adult return ( $n = 47$ , adjusted  $R^2 = 0.56$ , overall  $P < 0.001$ ,  $P(\text{SW1} + \text{SW2}) <$



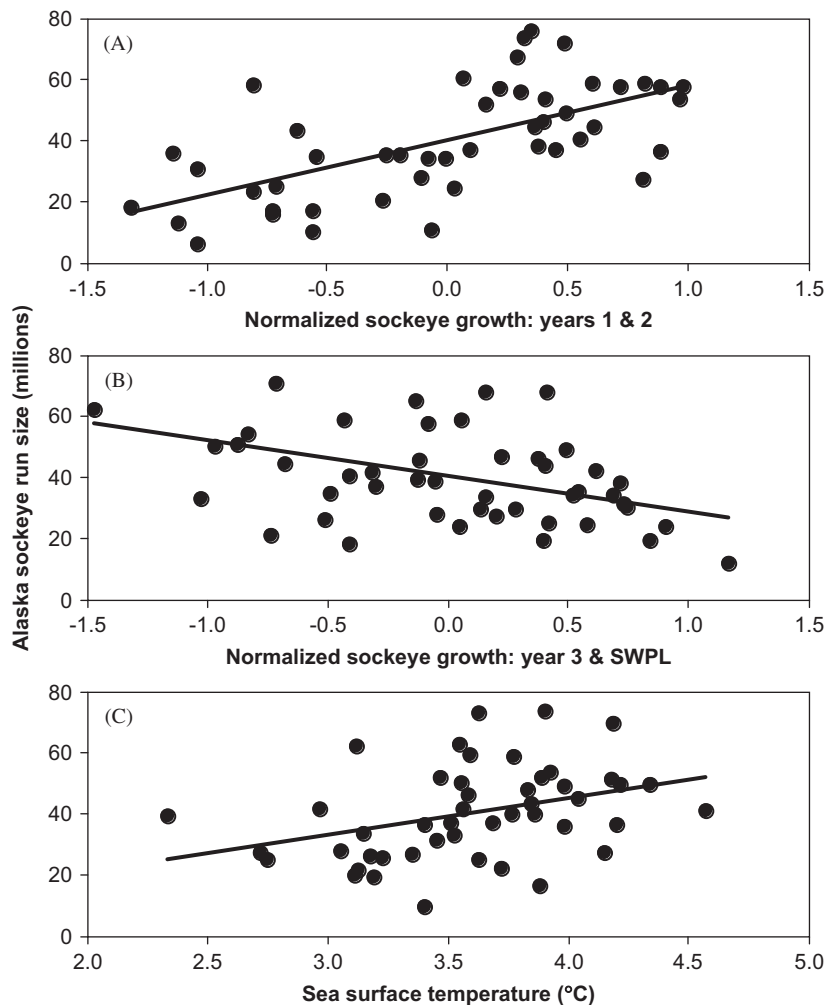


Fig. 4. Multivariate relationship showing the effect on annual sockeye salmon run size (western and central Alaska) of salmon scale growth during first 2 years at sea (A), scale growth during the third year at sea and homeward migration (B), and mean SST prior to smolt migration (January–April) (C), years 1955–2001. Abundance values are partial residuals of Eq. (1) (see text).

0.001,  $P(\text{SW3} + \text{SWPL}) = 0.017$ ,  $P$  (pink salmon index) = 0.028,  $P(\text{SST}) = 0.020$ . Autocorrelation and partial autocorrelation of model residuals were non-significant at lags 1–6 ( $P > 0.05$ ). When abundance was regressed on early marine growth only, the residuals from this model show significant first-order (lag 1) autocorrelation. Using both early and late marine growth in the same model, autocorrelation in the residual terms is avoided. Furthermore, having both terms in the statistical model as predictors also allowed us to check for collinearity, which was negligible, e.g., VIF values were 1.1–1.8.

Approximately 56% of the variability in annual sockeye salmon abundance in western and central

Alaska during 1955–2001 was explained by the model. Standardized regression coefficients indicated that growth during the first 2 years at sea had the greatest influence on sockeye salmon abundance in the model, followed in descending order of influence, by growth during the last two seasons at sea, pink salmon abundance, and SST. SSTs during the period of ocean entry and residence (May–August) were not correlated with salmon abundance after growth was incorporated into the model. The time series of model residuals did not reveal additional patterns associated with climate shifts, but 1972 and 1997 were approximately two standard deviations less than model expectations. SST was exceptionally cold

during the winters of 1971 and 1972, and 1997 was exceptionally warm during summer (Stabeno et al., 2001; Overland and Stabeno, 2004).

### 3.3. Salmon growth, productivity, and density dependence

The Bristol Bay sockeye salmon productivity index was positively correlated with Bristol Bay sockeye salmon scale growth during the first 2 years at sea, but negatively correlated with scale growth during the third year at sea (Fig. 5):

$$\text{SR index } (R/S)_j = -1.326 + 1.422(\text{SW1} + \text{SW2})_j - 1.009(\text{SW3})_j, \quad (2)$$

where  $j$  is the parent spawning year ( $n = 46$ , adjusted  $R^2 = 0.36$ , overall  $P < 0.001$ ,  $P(\text{SW1} + \text{SW2}) = 0.002$ ,  $P(\text{SW3}) = 0.012$ ). Autocorrelation of model residuals was non-significant at lags 1–6 ( $P > 0.05$ ) and diagnostic tests indicated that collinearity among independent variables was negligible, e.g., VIF values were 1.1. An alternative model was developed that utilized growth during each of the first and second years at sea, but the effects of each year on productivity were similar. Average SST in the southeastern Bering Sea from January to August of

the year of ocean entry did not add a statistically significant term to the model after salmon growth had been added ( $P > 0.05$ ), but winter/spring SST (i.e., mean corresponding with adjacent smolt years) was positively correlated with both salmon productivity ( $r = 0.45$ ) and SW1 scale growth ( $r = 0.37$ ). The effect of pink salmon abundance on sockeye salmon productivity was not tested because each cohort of sockeye salmon entered the ocean in both odd- and even-numbered years and therefore each cohort experienced both high and low abundances of pink salmon.

### 3.4. Sockeye salmon length, density dependence, and ocean climate regimes

The effect of the 1976–1977 and the 1989 ocean regime shifts on mean adult sockeye salmon length was examined by plotting the time series of residuals of the following model:

$$\text{Sockeye length (mm)}_i = 550.9 - 0.178(\text{sockeye abundance})_i - 0.144(\text{pink salmon catch})_{i-1}, \quad (3)$$

where  $i$  is year of returning salmon ( $n = 46$ , adjusted  $R^2 = 0.40$ , overall  $P < 0.001$ ,  $P(\text{sockeye abundance})$

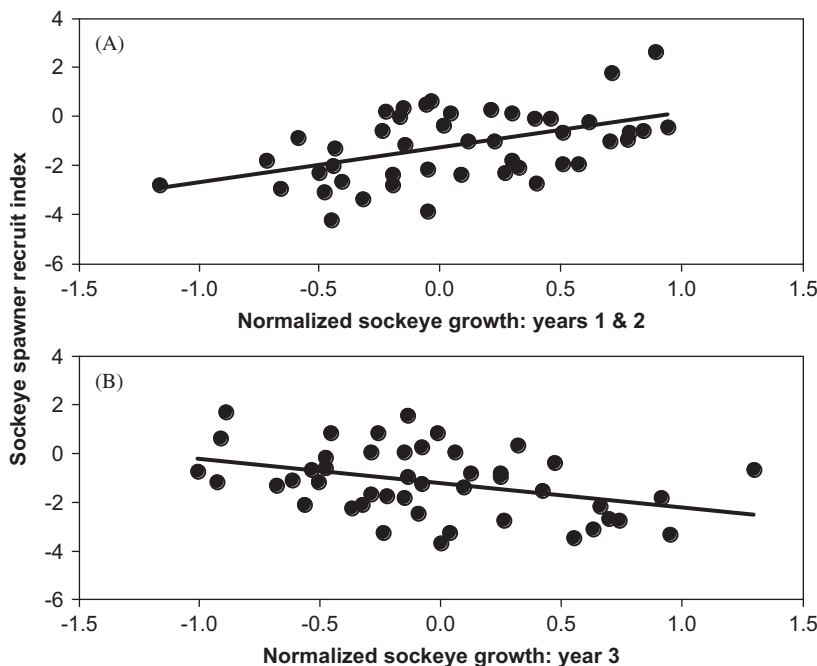


Fig. 5. Multivariate relationship showing the effect on productivity of Bristol Bay sockeye salmon (return per spawner residual) of salmon scale growth during first 2 years at sea (A), and scale growth during the third year at sea (B), cohort years 1952–1997. Productivity values are partial residuals of Eq. (2) (see text).

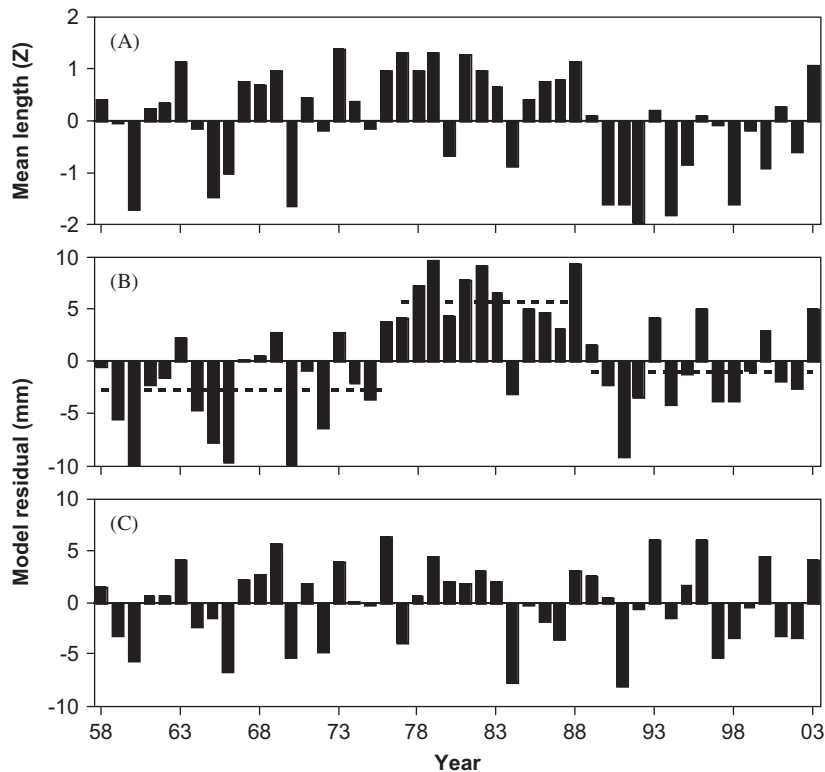


Fig. 6. Mean age-specific length of adult Bristol Bay sockeye salmon (A), and residuals of multivariate models that predict adult length from sockeye and pink salmon abundances: (B) prior to inclusion of regime shift effects, and (C) after inclusion of regime shift effects. Dash line highlights mean residual during regime periods before inclusion of its effect in model.

= 0.001,  $P$  (eastern Kamchatka pink salmon catch) < 0.001). Residuals from this model showed three distinct periods of adult sockeye salmon size after removing effects of sockeye and pink salmon abundance: relatively small size during 1958–1975, greater size during 1976–1988, and moderate size during 1989–2003 (Fig. 6B). The transitions in adult length shown in model residuals corresponded with the 1976–1977 and 1989 ocean regime shifts and indicated adult salmon length responded rapidly to conditions associated with the climate shifts after accounting for intra- and interspecific competition.

Effects of the 1976/1977 and 1989 ocean regime shifts were incorporated into the final Bristol Bay adult length model (Fig. 7):

$$\begin{aligned} \text{Sockeye length (mm)}_i = & 550.0 - 0.275(\text{sockeye abundance})_i \\ & - 0.170(\text{pink salmon catch})_{i-1} \\ & + 10.3(\text{period : 1977 - 1988}) \\ & + 4.4(\text{period : 1989 - 2003}), \end{aligned} \quad (4)$$

where regime period 1977–1988 was coded “1”, regime period 1989–2003 was coded “1” and 1958–1976 was always coded “0”;  $n = 46$ , adjusted  $R^2 = 0.68$ , overall  $P < 0.001$ ,  $P$  (sockeye abundance) < 0.001,  $P$  (eastern Kamchatka pink salmon catch) < 0.001,  $P$  (period 1977–1988) < 0.001, and  $P$  (period 1989–2003) = 0.019. Autocorrelation of residuals was non-significant at lags 1–6 ( $P > 0.05$ ) and collinearity among independent variables was minimal (VIF = 1.3–2.0). Model residuals indicated that body length during 1997 and 2001–2003 (unusual climate conditions) were not outliers (Fig. 6C). Adult salmon length tended to be exceptionally small following the 1989 climate shift (Fig. 6A) due to relatively low growth during late marine life, especially during odd-numbered years (Fig. 2).

Partial residual plots show that adult sockeye salmon length was inversely related to adult sockeye salmon abundance and to the index of Asian pink salmon abundance during the previous year (Fig. 7). Pink salmon abundance during the year prior to

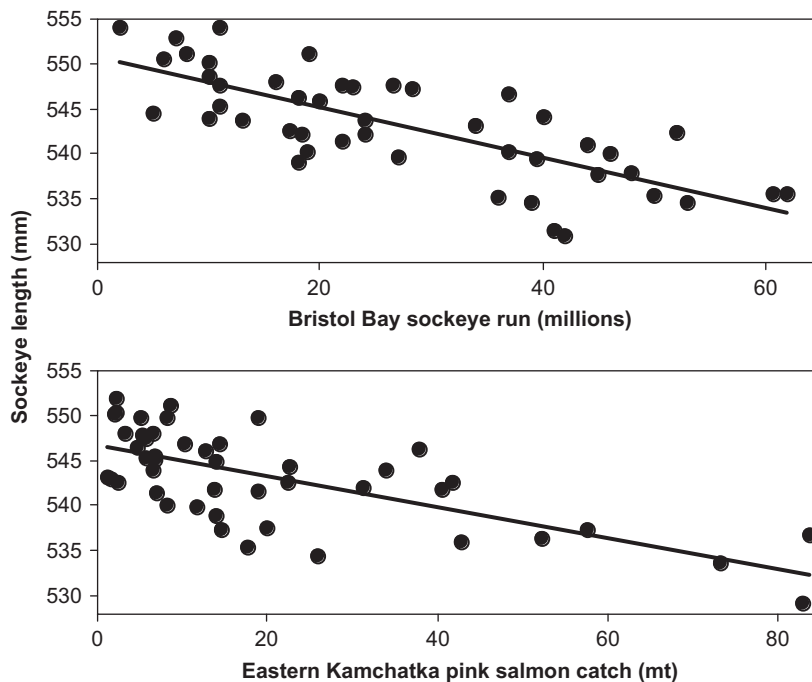


Fig. 7. Effects of adult Bristol Bay sockeye salmon abundance (A) and eastern Kamchatka pink salmon catch during the previous year (B) on mean adult length at age of Bristol Bay sockeye salmon, 1958–2003. Relationships show the effect of each variable, based on partial residual analysis, after incorporating effects of other variables in Eq. (4) (see text).

homeward migration was used in the model because little interaction with Asian pink salmon occurs during homeward migration (Ruggerone et al., 2003). Thus, density-dependent effects on adult sockeye salmon size were significant during late life stages. SST in the North Pacific Ocean (47–55°N; 172°E–140°W) during winter prior to the homeward migration did not add significant new information to the model ( $P = 0.105$ ).

#### 4. Discussion

The key finding of this study was that abundance of western and central Alaska adult sockeye salmon and productivity of Bristol Bay sockeye salmon during the past 45 years were positively correlated with scale growth during the first 2 years at sea. Sockeye salmon productivity was negatively correlated with growth during the third year at sea and during homeward migration. Faster growth during the first 2 years at sea and slower growth during later life stages tended to occur after the 1976–1977 climate shift. Shifts in age-specific adult length of Bristol Bay sockeye salmon were associated with the 1976–1977 and 1989 climate shifts after accounting

for intraspecific competition among maturing Bristol Bay salmon and interspecific competition with Asian pink salmon. We interpret these results as an indication that greater growth of sockeye salmon during early marine life enhanced survival and abundance, which in turn led to reduced growth during later life stages when growth-related mortality was less likely.

These findings suggest a mechanism to explain reduced adult body size of Pacific salmon in northern areas during the past 30 years (Bigler et al., 1996; Kaeriyama, 1998; Pyper and Peterman, 1999) in light of what has been assumed to be a period of high biomass of salmon prey (e.g., zooplankton in the North Pacific Ocean: Brodeur and Ware, 1992). Some researchers suspected that density-dependent growth occurred primarily during late life stages (Rogers, 1980; McKinnell, 1995; Percy et al., 1999), but others suggested density-dependent growth also occurred during early marine life (Peterman, 1984; Ishida et al., 1998). Our findings show that salmon growth trends at sea can vary by life stage, apparently in response to ontogenetic shifts in prey selection (Davis, 2003), changes in prey biomass, and climate change. In

northern regions where the abundance of sockeye salmon has been relatively great, it was density-dependent growth during late marine stages that contributed to smaller size at maturity. We did not detect density-dependent growth during early marine life before or after the climate shift in the mid-1970s; e.g., growth of sockeye salmon was relatively high immediately after entry into Bristol Bay following the climate shift (Ruggerone et al., 2005). For salmon populations in more southern regions (Canada, Pacific Northwest, and California), where many stocks are now depressed, it is possible that growth during both early and late marine life was low (Bigler et al., 1996; Hobday and Boehlert, 2001; Ruggerone and Goetz, 2004; Wells et al., 2006).

Salmon growth is largely regulated by prey availability and temperature, which influence metabolic efficiency in converting food to body weight (Brett, 1995). Davis et al. (1998) modeled the bioenergetics of salmon in the ocean and concluded that prey availability rather than temperature governed salmon growth rate within the relatively narrow temperature range encountered by northern salmon populations during summer; i.e., 5–9 °C in the Bering Sea and 5–11 °C in central North Pacific Ocean. In more southern areas, relatively high temperatures may have constrained salmon growth efficiency and reduced size in recent years (Welch et al., 1995; Cox and Hinch, 1997), although salmon also have the ability to dive into deeper, cooler waters (Walker et al., 2000) which may enhance growth efficiency (Brett, 1995).

We found that regionally averaged SST during early marine life had a weak influence on adult salmon abundance after accounting for growth at sea, a finding consistent with Davis et al. (1998). Seo et al. (2006) reported that annual scale growth of chum salmon in the Bering Sea was better correlated with zooplankton biomass than SST. SST appears to be associated with salmon abundance and productivity (Mueter et al., 2002) largely through its effects on prey availability. Evidence that prey availability is key to salmon growth in northern areas is important because there is a paucity of continuous long-term data on the abundance of salmon prey in the ocean.

The time series of annual scale growth of sockeye salmon in the Bering Sea and the Gulf of Alaska supports hypotheses that abundances of lower trophic level species consumed by sockeye salmon increased in both regions after the mid-1970s in

association with warmer temperatures (Francis et al., 1998; Hunt et al., 2002; Trites et al., 2007). However, increased growth of sockeye salmon during early marine life in the Bering Sea did not reflect the relatively stable zooplankton biomass (Napp et al., 2002), either because sockeye salmon consumed a variety of prey whose abundance was not accurately measured by zooplankton sampling gear (Percy et al., 1988; Cooney and Brodeur, 1998) or because zooplankton productivity was high and numerous salmon grazed zooplankton biomass down to pre-1977 levels. Greater growth of sockeye salmon during early marine life and immediately after the climate shift may have been related to the large increase in age-0 pollock (Hunt et al., 2002), a species that can be exceptionally abundant in the diet of juvenile sockeye salmon on the eastern Bering Sea shelf (Farley et al., 2005). Because older sockeye salmon consume small fishes (Davis, 2003), we hypothesize that relatively low sockeye salmon growth during late marine life after the 1976/1977 and 1989 climate shifts may have been exacerbated by the decline in forage fishes, including age-1 pollock, since the late 1970s (Hunt et al., 2002).

Salmon growth during the third year at sea and homeward migration declined during periods when sockeye and pink salmon became abundant. Such density-dependent growth is more likely to be observed during later life stages of salmon when adult body size is largely determined (Brett, 1995). During the last 4 months of ocean life, salmon consume a volume of prey that typically equals the sum of all prey consumed during all previous months, and body weight typically doubles during the last 5–6 months of ocean life (Brett, 1995). The efficiency of converting food to body mass decreases as salmon age, indicating the need for increasing food intake to maintain growth rate. A small reduction in daily consumption by salmon in the ocean can lead to significant decline in body weight (Davis et al., 1998). Although reduced growth during the second year at sea can significantly lower salmon survival (Ruggerone et al., 2003), the effect of reduced growth on survival during the third year and homeward migration is likely less (Ricker, 1976).

Reduced growth during late life stages may significantly affect salmon productivity by affecting their reproductive potential and success. Rapid growth at sea is directed in part toward storage of energy reserves. During last stages of maturation,



female salmon partition approximately 12–15% of body mass into the ovary while utilizing approximately 98% of somatic fats (Brett, 1995). As salmon approach freshwater, they stop feeding even though they have significant energy requirements for upstream migration, selections of mates, and building and defending nests. Some energy is derived from protein catabolism. Egg size and egg number are determined late during the maturation process and both decline with smaller salmon body size (Quinn et al., 2004). Smaller eggs produce smaller fry, which are more vulnerable to predation compared with larger fry (Ruggerone and Rogers, 1992). Thus, density-dependent growth during the third year at sea and homeward migration may significantly affect salmon reproductive potential and future productivity. It is noteworthy that the decline in productivity of several Bristol Bay sockeye populations that began in 1991 closely corresponded with the decline in adult size after the 1989 climate shift. Downton and Miller (1998) suggested that warmer SST during the return migration may lower the reproductive success of Alaska sockeye salmon, and Crossin et al. (2004) reported that somatic energy of returning Fraser River sockeye salmon was influenced by climate regimes. Thus, density-dependent growth and SST may influence the reproductive potential of the returning parents, whereas growth during early marine life is key to salmon survival.

Biologists have long suggested that greater smolt size (Henderson and Cass, 1991) and/or greater growth at sea can lead to greater survival of Pacific salmon, either in response to lower predation rates (Fisher and Percy, 1988; Holtby et al., 1990; Willette, 2001) or reduced growth-related mortality (Nagasawa, 2000; Beamish and Mahnken, 2001). Our findings support these hypotheses. Recent growth and survival studies of Bristol Bay sockeye salmon have indicated that competition by Asian pink salmon reduced sockeye salmon growth at sea during odd-numbered years, leading to a 26–45% reduction in survival depending on freshwater age (Ruggerone et al., 2003). Seasonal scale-growth trends indicated that growth was reduced in response to competition with pink salmon after spring and reduced growth continued through summer and fall (Ruggerone et al., 2005). These authors hypothesized that high feeding rates of pink salmon during spring and early summer, coupled with declining zooplankton biomass during summer, and potentially cyclic abundances of other

prey, contributed to reduced growth of Bristol Bay sockeye salmon during late spring through fall of odd-numbered years.

Studies have demonstrated that salmon populations respond to regional climate and ocean conditions, including SST (Mueter et al., 2002; Pyper et al., 2005). Our investigation of Bristol Bay and Chignik salmon scales indicated both regional and broad scale responses of salmon to climate change. For example, both Bristol Bay and Chignik salmon exhibited greater early marine growth followed by reduced late marine growth after the 1976/1977 regime shift. However, the response of Chignik sockeye salmon to the regime shift was much more pronounced during the first 2 years at sea and less pronounced during the third year at sea compared with Bristol Bay salmon. In contrast to Bristol Bay salmon, Chignik salmon did not exhibit an alternating-year pattern of growth during the second year at sea. These patterns likely reflect different ocean distributions of Chignik and Bristol Bay salmon. Although they overlap considerably after the first year at sea (Myers et al., 1996), Chignik salmon tend to be distributed farther east where the influence of alternating-year abundances of Asian pink salmon is less.

Little is known about predator (top down) effects on salmon abundance in relation to climate change, although the abundance of salmon sharks (*Lamna ditropis*) increased after 1995 (Nagasawa, 1998; Nagasawa et al., 2002). In the Pacific Northwest, analysis of 53 million tagged juvenile chinook salmon over a 25-year period indicated the mechanism of mortality shifted from primarily predation to primarily competition in response to climate change that affected predator abundance, competitor abundance, and prey availability (Ruggerone and Goetz, 2004). In this region, recent warm temperatures were associated with fewer predators, fewer preys, and more competitors. Although evidence is increasing that growth of salmon is key to salmon survival at sea, there is little direct evidence indicating whether size-selective predation or growth-mediated mortality during winter is most important during cold or warm climate regimes.

Our observations contribute to the ongoing exploration of hypotheses on the mechanisms that link ecosystem responses to climate change (Beamish, 1993; Francis et al., 1998; Hunt et al., 2002) because few long-term datasets of annual prey biomass, growth and survival are available for marine animals. The cold regime prior to the

mid-1970s was associated with both low early marine growth and low abundance of sockeye salmon, apparently in response to low prey availability (Brodeur and Ware, 1992; Davis et al., 1998) and possibly to colder SSTs. After the climate shift, early marine growth and abundance of salmon increased, indicating availability of salmon prey also increased. During both regimes, density-dependent growth was apparent during the second and third years at sea and during homeward migration, indicating that salmon abundance was sufficient to affect prey populations during both cold and warm periods (Ruggerone et al., 2003, 2005). These observations highlight the complex dynamics of species interactions that change as salmon grow and mature in the ocean.

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